Schultz's rule in domesticated mammals

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Abstract

Schultz's rule predicts early eruption of replacement teeth (incisors, canines, and premolars) relative to molars as growth slows and life history events take place over a greater span of time. Here, we investigate if the opposite trend might occur during the domestication process as a consequence of an accelerated life-history and driven by increased energetic needs. We provide new data on tooth eruption in four mammalian species and their domesticated forms: wolf and dog, polecat and ferret, bezoar and goat, wild boar and pig. Our results show some variation in eruption sequences between wild and domestic forms, but none that is consistent and reliably distinct from intraspecific variation. There may be variation in the absolute timing of dental eruption, but despite well documented changes across life history variables, which distinguish wild from domestic forms, eruption sequences remained constant in each wild and domestic version of the species we examined. A conserved eruption sequence is in accordance with many earlier studies, which found no evidence for Schultz's rule in some wild clades of mammals. Phylogenetic conservation and functional factors likely play an important role in constraining patterns of growth and tooth eruption in these mammals. Furthermore, we suggest that the domestication processes started too recently for fundamental changes of tooth eruption sequences to occur.

Keywords Tooth eruption, Sequence, Domestication, Life history, Heterochrony

Introduction

According to Schultz (1956, 1960), life history is correlated with patterns of tooth eruption in mammals. Schultz's rule predicts that slow-growing mammals with a slow life history (e.g., late sexual maturity, long gestation and lifespan) tend to increase the number of replacement teeth (incisors, canines, premolars) erupting simultaneously with or before the molars; in more rapidly growing mammals with a faster life history on the other hand, the replacement teeth usually erupt only after most or all molars (Schultz, 1956, 1960; Smith, 2000) (Fig. 1). It has been hypothesised that a prolonged juvenile phase in slow-growing mammals makes necessary the relatively earlier replacement of the deciduous teeth to prevent them from wearing out before the permanent teeth become functional; alternatively, later eruption of the molars might be a consequence of a prolonged lifespan as a mechanism to keep the dentition functional for a longer period of time (Asher et al., 2017; Janis and Fortelius, 1988). Support for Schultz's rule has been found in primates and 'ungulates' (Henderson, 2007; Smith, 2000); weak evidence for Schultz's rule has been found in Hyracoidea (Asher et al., 2017); evidence is disputed in primates (Byrd, 1981; Godfrey et al., 2005; Guthrie and Frost, 2011; Jogahara and Natori, 2012; Monson and Hlusko, 2018a; Schwartz et al., 2005; Schwartz, 1974; Tattersall and Schwartz, 1974); and the rule seems not to apply in artiodactyls (Monson and Hlusko, 2018b; Veitschegger and Sánchez-Villagra, 2016). Several factors may augment and/or play a more important role in determining eruption patterns than Schultz's rule, such as phylogenetic history, jaw and tooth size, and mode of growth of jaws and teeth.

Domestication is relevant to Schultz's rule because marked changes of many life history variables have occurred independently in different species (Herre and Röhrs, 2013). Relative to the time elapsed from common ancestors of major clades (e.g., strepsirhines and haplorhines or suiforms and ruminants), domesticated forms occupy the tips of exceedingly short branches. This makes it possible to investigate how life history and dental eruption may correlate with one another, independent of phylogenetic constraints. Specifically, in domestic animals, many aspects of life history tend to be

faster compared to wild relatives, including earlier sexual maturity, larger litters, and more frequent and non-seasonal breeding (Herre and Röhrs, 2013; Tchernov and Horwitz, 1991)(see also Appendix A, Table A.1). This could be the effect of intentional artificial selection for increased productivity and/or the specific nature of the anthropogenic environment (Tchernov and Horwitz, 1991). Such environments are characterised by strong and unpredictable resource fluctuation, high intraspecific competition, low interspecific competition and predation, and isolation, all of which potentially favour adaptations towards a 'fast' life history (Hulme-Beaman et al., 2016; Tchernov and Horwitz, 1991). In the framework of Schultz's rule, one might therefore expect that faster growth and life history in domesticated mammals would result in later eruption of replacement teeth compared to molars relative to the wild forms (Fig. 1). Hence, if Schultz's rule were generally true among mammals, we would expect that molars erupt earlier relative to replacement teeth in domestic euungulates (i.e., perissodactyls and artiodactyls) and canids compared to their wild relatives (Fig. 1).

Our hypothesis about a reversed Schultz's rule in domestication was based on considerations concerning the correlation of tooth eruption and life history specific for domesticated mammals. Wild euungulates (i.e., perissodactyls and artiodactyls) tend to attain sexual maturity before their teeth and skeleton are fully grown (Shigehara, 1980; Smith, 1992). In addition to that, many domesticated euungulates attain sexual maturity even earlier than their wild relatives (e.g., Herre and Röhrs, 2013). As early sexual reproduction imposes considerable energetic cost, there might be selective pressure in at least some domesticated euungulates to erupt molars relatively early in order to increase the overall chewing surface and maximise mastication potential as early in life as possible (Geiger et al., 2018; Rodrigues et al., 2017).

Conversely, wild carnivorans tend to attain sexual maturity only after the skeleton and the teeth are fully grown (Shigehara, 1980; Smith, 1992). As in the euungulates, sexual maturity is usually attained earlier in the domesticated forms, but does not occur prior to the full eruption of all permanent teeth

(e.g., in domestic dogs; Geiger et al., 2016). Although sexual maturity might therefore not impose a selective pressure on tooth eruption, relatively early independence from food provisioning in domestic dogs compared to wolves probably does. This is exemplified by wolves, the wild relative of domestic dogs; when weaning starts, pack members regurgitate food to pups for up to one year (Lord et al., 2013). In contrast, domestic dog pups are rarely fed in this manner and become completely independent from their mother subsequent to weaning at about 10 – 11 weeks of age, when they start competing with other conspecifics for available food (Lord et al., 2013). At this age, none of the deciduous teeth are replaced and no molar is erupted (Habermehl, 1975; see also Appendix B). Since domestic dogs are more omnivorous than wolves (Axelsson et al., 2013), grinding surfaces of molars might be more important for the former than for the latter (Holliday and Steppan, 2004). In contrast, the carnivoran's shearing carnassial teeth (composed of the m1 and P4), the anterior premolars and the canine teeth are typically used for slicing meat and tendons, and holding and strangling prey, respectively (Hillson, 2005). These functions might be of lesser importance in the domestic environment. Earlier independence and greater importance of dental grinding surfaces in domestic dogs compared to wolves might imply a selection pressure for early molar eruption in domestic dogs in order to optimise energy intake. It is not clear whether similar considerations might also apply to solitary carnivorans with no extensive post-weaning food provisioning for the young, e.g., the ferret (Blandford, 1987).

Materials & Methods

To test this hypothesis, we used 148 skulls and mandibles representing ontogenetic series in the relevant stages of tooth eruption of four widespread domesticated species (e.g., Mason 1984) and their wild relatives: *Sus domesticus* (domestic pig, *N* = 23) and *Sus scrofa* (wild boar, *N* = 28), *Capra hircus* (domestic goat, *N* = 10) *and Capra aegagrus* (wild goat, or bezoar, *N* = 8), *Canis familiaris* (domestic dog, *N* = 22) and *Canis lupus* (wolf, *N* = 15), and *Mustela furo* (domestic ferret, *N* = 12) and *Mustela putorius* (European polecat, *N* = 26). Note that we consider the wild and the domestic form

as conspecifics, although given different scientific names (Gentry et al., 2004). Raw data from domestic dogs and wolves are in part from an earlier study (Geiger et al., 2016). Differences of tooth eruption sequences of another important domesticated species, as a consequence of domestication, the sheep (*Ovis*), are investigated and discussed in another place (Geiger et al., 2018). Additional information on the materials and methods are available in the Appendix A.

We used specimens of both sexes with a complete set of permanent teeth, as typical for the species (Hillson, 2005). All specimens are part of institutional collections: Palaeontological Institute and Museum of the University of Zurich, Switzerland (AvN), The Natural History Museum, London, United Kingdom (BMNH), Naturhistorisches Museum Basel, Switzerland (NMB), Naturhistorisches Museum Bern, Switzerland (NMBE), Naturhistoriska Riksmuseet, Stockholm, Sweden (NRM), Zoological Institute of the Russian Academy of Science, Saint-Petersburg, Russia (ZIN RAS), Museum für Naturkunde, Berlin, Germany (MfN), Zoologische Staatssammlung München, Germany (ZSM). The domestic dogs at NMBE are housed in the collection of the Albert-Heim-Foundation and the domesticated pigs at MfN are housed in the Nehring-Collection (Zoologische Sammlung der Königlichen Landwirtschaftlichen Hochschule zu Berlin).

We coded teeth of dry skulls (as opposed to CT-scans, see below) in the following stages: 1, Not erupted; the tooth is not yet erupted above the alveolar level, but might be visible in the crypt. 2, Erupting; the tooth has started to erupt and is at least in part above the alveolar level, but has not yet reached the occlusal plane. 3, Fully erupted; the tooth is fully erupted into occlusion (Geiger et al., 2016). The latter stage was determined according to first signs of wear, the attainment of a position of the crown in one line with other fully erupted teeth (in the occlusal plane), and the visibility of the enamel-dentin junction above the alveolar level, where applicable. Teeth of the lower jaw are denoted in lower case and teeth of the upper jaw in upper case (e.g., Asher et al., 2017; Gomes Rodrigues et al., 2017; Martin, 2005; Slaughter et al., 1974; Van Nievelt and Smith, 2005). I/i

131 indicates incisors, C/c canines, P/p premolars, M/m molars, and numerals represent each tooth
132 locus. The homology of the first premolar, present in *Canis* and *Sus* in this study, may be with the
133 deciduous generation (Ziegler, 1971). We therefore excluded this locus.
134
135 All skulls and mandibles comprise specimens in which at least one tooth is in stage 2. We chose the
136 sample so that the dentally most immature specimen in each group exhibits only one permanent
137 tooth in the process of eruption (stage 2) or completely erupted (stage 3), with the other teeth still in
138 their crypts (stage 1). (Note that this was not possible for *Mustela*, in which the dentally most
139 immature specimen had up to three permanent incisors already partly erupted. The incisors in this
140 species are comparatively small and appeared to start erupting simultaneously or closely timed, so
141 that we could not establish the sequence of eruption among incisors. However, this did not hamper
142 the object of this study, which is the comparison of the eruption sequence of molar and replacement
143 teeth.) Further, we included one specimen with a complete set of fully erupted permanent teeth
144 (except canine teeth, see Appendix A) in every group, available for all groups except the wild (and
145 rare) *Capra aegagrus*. This ensured a comparable set of growth stages for every group.
146
147 We then established the sequence of beginning and complete eruption in every wild and
148 domesticated group separately for the upper and the lower jaw. For this, we added the eruption
149 stages of all permanent tooth loci, resulting in a 'specimen eruption score' (ES). For example, a
150 domestic dog with lower i1 and i2 fully erupted (stage 3), i3, c, and m1 in the process of eruption
151 (stage 2), and p2, p3, p4, and m3 still in their crypts (stage 1) would attain an eruption score of 18 (3_{i1}
152 $+ 3_{i2} + 2_{i3} + 2_{c} + 1_{p2} + 1_{p3} + 1_{p4} + 2_{m1} + 2_{m2} + 1_{m3} = 18$). We then ordered the specimens in each wild and
153 domestic form according to their specimen's eruption score. Specimens with few erupting and
154 erupted teeth would have a smaller eruption score, whereas specimens with many erupting and
155 erupted teeth would have a larger eruption score and we assumed that the latter were older than
156 the former. This assumption has been validated on the basis of known age sheep (Geiger et al.,

2018). These ordered specimens could be used to visually assess the sequence of tooth eruption. For every tooth locus, we calculated the sum of all eruption stages over all specimens of a group (e.g., all values for m1 in the wolf) resulting in a 'tooth locus eruption score'. Thus, a tooth which erupts early (many specimens with stage 2 and 3 for that tooth) would attain a higher eruption score compared to a tooth which erupts late (many specimens with stage 1 for that tooth). These tooth locus eruption scores thus indicated the sequence of eruption by ordering the loci from the highest (erupted first) to the lowest (erupted last) eruption score. Together, specimen and tooth locus eruption scores served for a quantitative and a qualitative assessment of eruption sequences. All raw data are available as supplementary material (Appendix B).

We evaluated the similarity of eruption sequences in the wild and the domestic form by comparing the number of replacement teeth (incisors, canines, and premolars) erupting before or after the molar teeth. According to Schultz's rule, we would expect to find more replacement teeth erupting after the molars in the domestic *Capra*, *Sus*, *Canis*, and *Mustela* compared to the respective wild form (Smith, 2000). Differences of the eruption sequences between the wild and domestic forms were not considered if these differences resulted on the basis of simultaneous eruption of teeth in one form but not the other. We chose to use this procedure because ambiguous sequences may be the result of intra-group variation (i.e., deviations of the group-specific eruption sequence on an individual basis) and/or missing ontogenetic stages (see also below). Such missing data might lead to the appearance of an unresolved eruption sequence, which would in fact be resolved. Intra-group variation and missing ontogenetic stages might incorrectly convey a difference of eruption sequence between the wild and the domestic forms, which cannot be considered a result of the domestication process.

To test if the dental eruption sequences of the wild and the domestic forms are similar to one another, we added up eruption stages of all replacement teeth in each individual where M1 was

completely erupted ('replacement teeth eruption score'). The replacement teeth eruption scores of the wild group of each species was then compared to the scores in the respective domestic group using (non-parametric) Mann-Whitney-U-tests. As a measure of the effect size, Pearson's correlation coefficients were calculated as $r=z/\sqrt{N}$, where z is the standardised test statistic and N is the total sample size including both groups in every comparison. When molars erupt relatively early in relation to the replacement teeth in the domestic group of a species, it will exhibit lower replacement teeth eruption scores than the wild group of that species, because fewer replacement teeth are erupting or have already erupted. The same analysis was conducted for m1, M2, and m2. All analyses were conducted using Microsoft Excel 2016 and Past 3.21 (Hammer et al., 2001).

In addition to the visual evaluation of tooth eruption, we obtained micro-computed tomography scans (µCT-scans) from *Mustela* (domestic *M. furo*, *N* =11; wild *M. putorius*, *N* =7). We chose this sample on the basis of availability of a sufficient number of specimens in suitable ontogenetic stages. µCT-scans make it possible to evaluate eruption stages of permanent teeth that are hidden in the bony crypts or underneath deciduous teeth and also enable the assessment of crown mineralisation and root development. This in turn may provide more detailed information on tooth eruption stages and hence eruption sequences (Appendix A, Fig. A.1), although dental eruption and development are not tightly correlated in all taxa or individuals (Godfrey et al., 2005; Tattersall and Schwartz, 1974). We examined the development of teeth using the clipping plane tool in Drishti 2.6.4 (Limaye, 2012), which allows for flexible examination of teeth in different depths and at various angles within the dentary. For this, we extended and supplemented the coding system described above according to Brown and Chapman (1991a, b) and Asher et al. (2017) to also include assessment of internal growth and developmental processes via µCT-scans (Appendix A, Table A.2, Fig. A.1). We used only lower jaws for these examinations due to a greater number of teeth in the lower jaws of *Mustela* (Hillson, 2005).

Results

Our data showed that the sequence of eruption of molars and replacement teeth are similar in the wild and the domestic group in each of the investigated species (Fig. 2). This result was underpinned by the Mann-Whitney-U-tests. The comparisons of replacement teeth eruption scores between wild and domestic pairs in all investigated species showed that there are no significant differences between the groups (Pearson's coefficients of variation $r<0.4$ and significance values $p>0.05$ for all comparisons). That is, the number of replacement teeth erupting or being erupted once M1, m1, M2 and/or m2 have erupted is no different in the domestic groups relative to their wild relatives. Similarly, the examination of µCT-scans in *Mustela* showed no evidence for a shift in eruption sequence between the wild and the domestic form. On the contrary, specimens of the wild and the domestic groups taken together complement a uniform sequence of tooth development and growth and underpin the similarity of eruption sequences in wild and domestic pairs (Appendix A, Fig. A.2)

Detailed examination of the sequences revealed intra-group variation, i.e., differences of dental eruption patterns among individuals within groups (wild and domestic), and sampling biases (Fig. 2a). Intra-group variation is apparent in cases where one tooth may start erupting or be completely erupted before another tooth in one specimen, while the configuration is the other way around in another specimen of the same group (e.g., I3 in stage 1 and C in stage 2 in one wild boar specimen exhibiting a 'specimen eruption score' (ES) of 12, and I3 in stage 2 and C in stage 1 in another wild boar specimen exhibiting ES 13, Fig. 2a). Such different configurations might even result in the same ES among specimens, despite different teeth exhibiting different eruption stages (e.g., multiple configurations of erupting/erupted teeth result in an ES of 16 in the upper jaw of domestic dogs, Fig. 2a). Sampling biases, on the other hand, are to be expected as samples may not represent the same age stages in the wild and the domestic group of a species. Therefore, resolution of tooth eruption sequences may vary between groups. For example, age stages in which all replacement teeth but not m3 are fully erupted were available for the domestic goat but not for the wild bezoar, leading to

different classification of i3 relative to m3 in the sequence. Furthermore, we could investigate a greater number of domestic dogs with starting eruption of the incisors, whereas such specimens were scarcer in our wolf sample, thus leading to different classification of the incisors and the first molar in the sequences. Lastly, in the wild polecat and the domestic ferret m1 is starting to erupt before m2, but due to the tiny size of the latter (Appendix A, Figure A.1), m2 may be fully erupted earlier than m1 in some individuals. (Note that relative tooth size is similar in each wild and domestic pair). Such intra-group variation may lead to ambiguity and/or unresolved eruption sequences, in turn leading to seemingly different eruption sequences, which are actually not based on the wild-domestic dichotomy. Intra-specific variation of dental eruption sequences has also been reported in wild mammals of various different clades (e.g., Forasiepi and Sánchez-Villagra, 2014; Monson and Hlusko, 2018a; Veitschegger and Sánchez-Villagra, 2016).

Discussion

In summary, our results show no evidence for a change of tooth eruption sequences of molar and replacement teeth between wild and domestic pairs of some of humanity's most ubiquitous domesticated species, *Canis*, *Mustela*, *Capra*, and *Sus*. Similar tooth eruption sequences have also been found previously in wild and domestic sheep (*Ovis*) (Geiger et al., 2018). Therefore, our data do not support Schultz's rule among domestic relative to wild groups. This is despite marked changes in life history (Appendix A, Table A.1), which would potentially lead to selection pressures towards relatively early molar eruption according to Schultz's rule (Fig. 1). However, the chronology of tooth eruption in days post-birth, as opposed to the sequence by which individual teeth erupt, can differ in wild vs. domestic groups of the same species, as shown recently for *Ovis* (Geiger et al., 2018). Schultz's rule may play a role behind such trends.

Our results are consistent with previous findings that phylogenetic conservation plays a key role in tooth eruption sequences, independent of life history (see above). Additional, non-exclusive factors

261 behind dental eruption are discussed below: (1) size, ontogenetic, or functional constraints, including
262 developmental canalization (Flatt, 2005); (2) potential absence of strong directional selection for a
263 change in eruption patterns; (3) a lack of a sufficient number of generations for changes to become
264 evident.
265
266 First, the high abrasiveness of plant material consumed by grazers likely poses considerable stress on
267 the low-crowned deciduous premolars. Replacing the premolars relatively early might therefore be
268 an adaptive advantage and molars will not erupt relatively earlier in domesticated caprines,
269 whatever the pace of their life history may be (Böhmer et al., 2016). In addition, size constraints
270 imposed by a correlated growth of the jaws and the dentition might not leave enough room for
271 molars to erupt considerably earlier in caprines (Geiger et al., 2018). In carnivorans, the deciduous
272 and permanent carnassial complexes (dP3/dp4 and P4/m1) might constrain the variation of tooth
273 eruption patterns as these teeth need to erupt in concert in order to function (Slaughter et al., 1974).
274 Despite the possibly reduced significance of these shearing teeth for domestic carnivorans, such
275 constraints might limit the potential to change the eruption sequence. Finally, small teeth might
276 erupt earlier than larger ones, simply because they need less time to reach the occlusal plane and
277 become functional. This might not be related to life history but to functional adaptations of dental
278 shape and size to a specific ecological niche.
279
280 Second, even without such constraints, there may not be directional selection for a change of tooth
281 eruption sequences in domestication. For example, Schultz's rule could still be a valid concept to
282 describe the correlated evolution of life history and tooth eruption sequences in mammals; however,
283 changes of life history that are observed in domestication (Appendix A, Table A.1), although marked,
284 are not substantial enough to result in any changes of the tooth eruption sequences.
285

Third, domestication is a relatively recent process in evolutionary timescales. Even the domestication of dogs, which is likely the oldest domestication event, started 14,000 to 40,000 years before present (Frantz et al., 2016; Botigué et al., 2017; for a review of earlier studies see Larson & Bradley, 2014). This is comparatively recent relative to the evolutionary timescales in which Schultz's rule is normally observed (e.g., as discussed by Smith, 2000) . Such short timescales coupled with evolutionary rates of phenotypic traits, which are not necessarily accelerated in domestication relative to the wild state (Geiger and Sánchez-Villagra, 2018; Purugganan and Fuller, 2011), might be too short for any substantial changes to the generally conserved dental eruption sequence to occur.

Our findings can nonetheless help to get a better grasp of the timeframes in which evolutionary changes of tooth eruption sequence can occur in nature. This is exemplified by *Myotragus,* a Plio-Pleistocene caprine that inhabited the Balearic Islands for 5.2 Ma and which evolved a set of apomorphies not found in mainland caprines (Köhler and Moyà-Solà, 2004). These peculiarities include a relatively late eruption of m3 and early eruption of the incisor (Bover and Alcover, 1999; Jordana et al., 2013). This sequence of tooth eruption is probably associated with a general slowdown of growth and life history in the context of its island environment, which is characterised by scarce resources and low extrinsic mortality, and is in accordance with Schultz's rule (Jordana et al., 2013; Köhler and Moyà-Solà, 2009). If sexual maturity is used as a measure for generation time, and given sexual maturity in *Myotragus* around 8-12 years (Köhler and Moyà-Solà, 2009; Marín-Moratalla et al., 2011), the *Myotragus* lineage evolved this changed eruption sequence over about 540k generations. This is an order of magnitude greater than the number of generations since a 40K-year origin of canid domestication. Dogs attain sexual maturity with on average one year (Johnston et al., 2001), which would result in a maximum of 40k generations since domestication. This comparison shows that if Schultz's rule is a valid concept to describe the correlated evolution of life history and tooth eruption sequence in these domesticated species, the number of generations

needed for such changes to occur might be much greater than has elapsed so far among domesticates.

Conclusions

To conclude, we found no evidence for significant changes to tooth eruption sequences in key domestic mammals, despite marked changes of life history that occurred independently during the domestication process. This result is consistent with some previous findings in other clades and highlights the conserved nature of dental eruption sequences, which show strong correlations with phylogenetic, functional, and size constraints. A study of Schultz's rule across all of Mammalia would be important to assess its general validity and would also help to establish its potential to infer life history in extinct forms (Asher et al., 2017; Böhmer et al., 2016; Domingo et al., 2018; Hellmund, 2013, 2016; Jordana et al., 2013; King et al., 2001; McGee and Turnbull, 2010; Miller et al., 2018; Sallam et al., 2016; Schwartz et al., 2005; Veitschegger et al., 2019). Future studies would also benefit from an expanded sample of rare juvenile specimens representing the missing ontogenetic stages. Considering dental eruption sequences of archaeological specimens representing more basal domestication stages was not possible in the current study, but would give further rigor to our results and would also broaden the taxonomic sampling, as domestic forms with extinct wild relatives could be added to these investigations (e.g., cattle and aurochs, see Appendix A). Finally, more detailed quantification of dental growth might reveal more subtle changes of tooth eruption between groups.

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Declarations of interest

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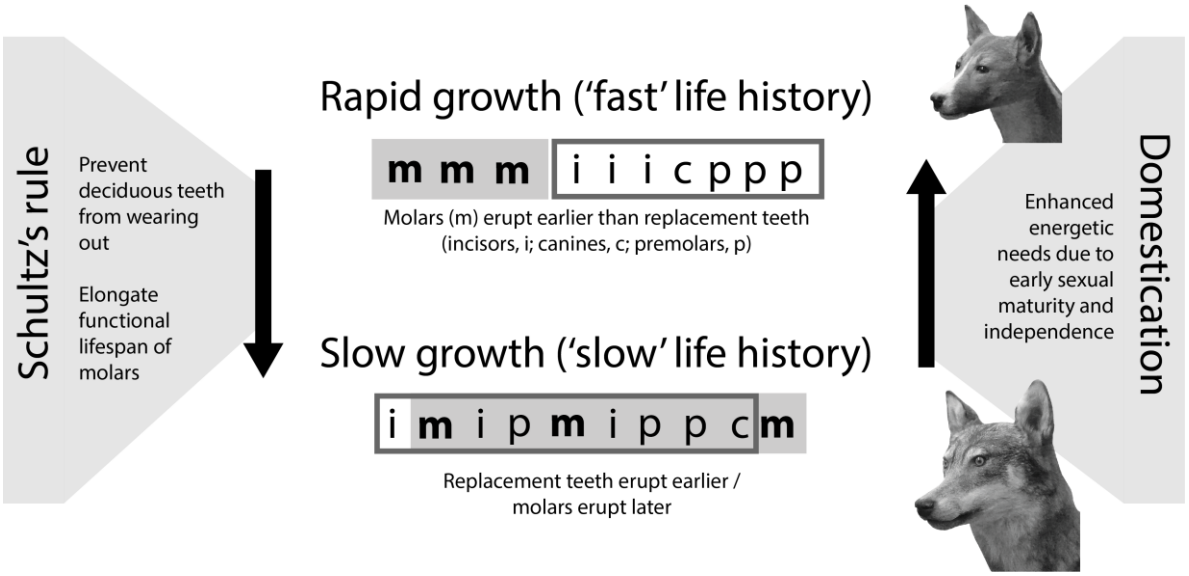
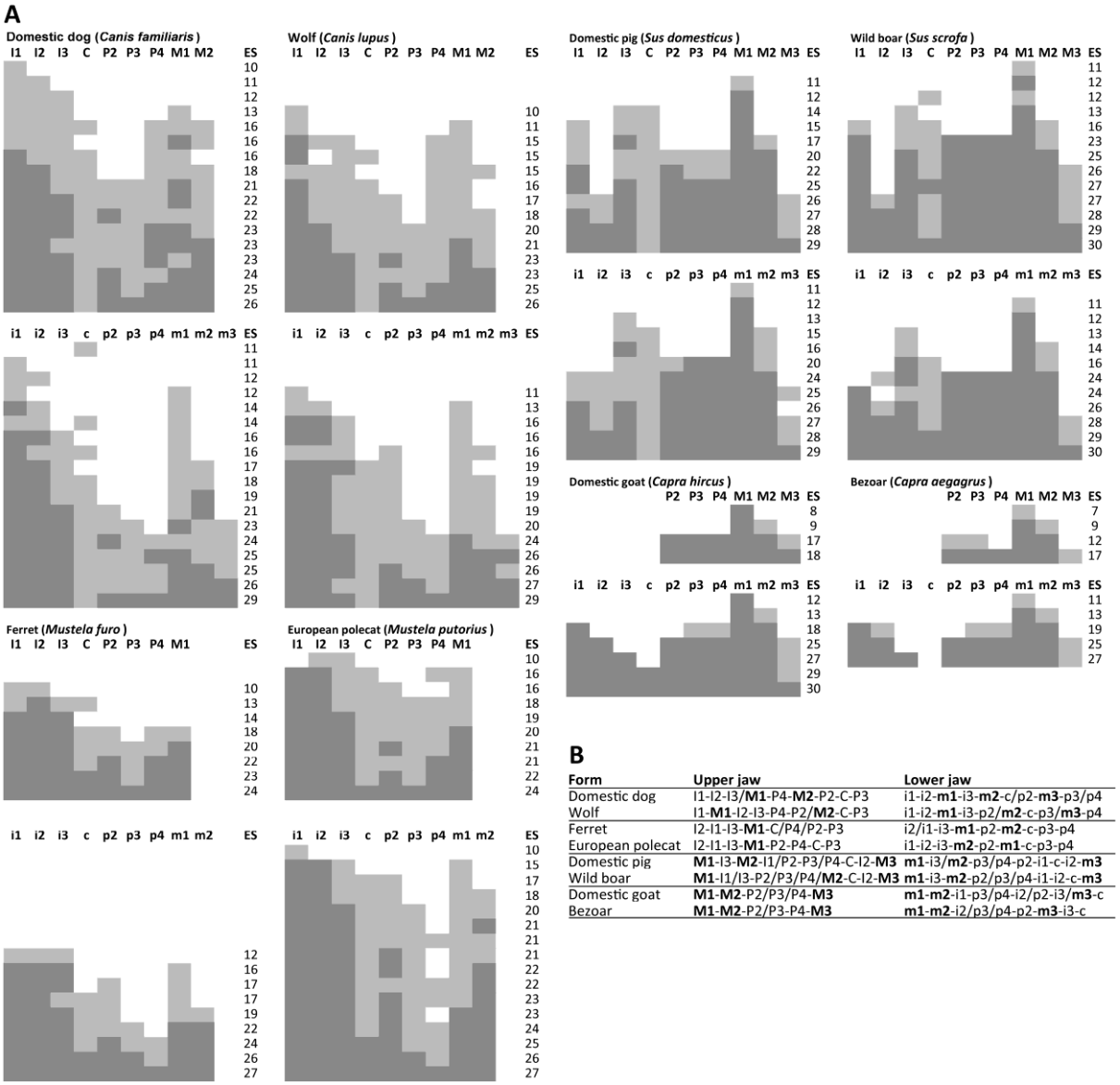


497

498 **Figure 1. Model of Schultz's rule and hypothetical changes associated with the domestication**
499 **process.** The schematic model shows the hypothetical adaptations of the tooth eruption sequences
500 as growth and life history tends towards the slower (left arrow; classical Schultz's rule; Smith, 2000)
501 and the faster (right arrow; domestication process; this study) end of the continuum. Modified after
502 Smith (2000).



Form	Upper jaw	Lower jaw
Domestic dog	I1-I2-I3/**M1**-P4-**M2**-P2-C-P3	i1-i2-**m1**-i3-**m2**-c/p2-**m3**-p3/p4
Wolf	I1-**M1**-I2-I3-P4-P2/**M2**-C-P3	i1-i2-**m1**-i3-p2/**m2**-c-p3/**m3**-p4
Ferret	I2-I1-I3-**M1**-C/P4/P2-P3	i2/i1-i3-**m1**-p2-**m2**-c-p3-p4
European polecat	I2-I1-I3-**M1**-P2-P4-C-P3	i1-i2-i3-**m2**-p2-**m1**-c-p3-p4
Domestic pig	**M1**-I3-**M2**-I1/P2-P3/P4-C-I2-**M3**	**m1**-i3/**m2**-p3/p4-p2-i1-c-i2-**m3**
Wild boar	**M1**-I1/I3-P2/P3/P4/**M2**-C-I2-**M3**	**m1**-i3-**m2**-p2/p3/p4-i1-i2-c-**m3**
Domestic goat	**M1**-**M2**-P2/P3/P4-**M3**	**m1**-**m2**-i1-p3/p4-i2/p2-i3/**m3**-c
Bezoar	**M1**-**M2**-P2/P3-P4-**M3**	**m1**-**m2**-i2/p3/p4-p2-**m3**-i3-c

Figure 2. Heat maps of tooth eruption in wild and domestic pairs (A). Columns indicate tooth loci and 'specimen eruption scores' (ES) that could be sampled in every group. ES were calculated by adding up eruption stages (see below and main text) of all permanent tooth loci for each specimen. Each row indicates a single observed ES, represented by at least one specimens. In cases where an ES was attained via different eruption stages for different loci (intra-group, i.e., individual, variation; see main text), more than one row represents one ES (e.g., ES 16 in the upper jaw of domestic dogs). Shading of eruption scores is as follows: white = stage 1 (not erupted), light grey = stage 2 (part erupted), dark grey = stage 3 (fully erupted and in occlusion). Note that not the same ES are represented in all groups and that differences in the sample size influence the resolution of the sequences. Eruption sequences were computed from 'tooth locus eruption scores' and dashes

indicate a resolved sequence between loci and slashed an unresolved/simultaneous eruption (B). The data indicate that there is no shift between molars and replacement teeth in the wild and domestic pairs according to Schultz's rule.

Supplementary information captions

Appendix A. Contains additional information on the used materials and methods, as well as Tables A.1 – A.2 and Figures A.1 – A.2.

Appendix B. Contains raw data, including all used specimens, their specifics, and their dental eruption stages.